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Remote Sensing of Environment

DOI: 10.1016/j.rse.2021.112464

Published: 01/07/2021

Peer reviewed version

Cyswllt i'r cyhoeddiad / Link to publication

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA): Adnan, S., Maltamo, M., Mehtätalo, L., Ammaturo, R. N. L., Packalen, P., & Valbuena, R. (2021). Determining maximum entropy in 3D remote sensing height distributions and using it to improve aboveground biomass modelling via stratification. Remote Sensing of Environment, 260, 112464. https://doi.org/10.1016/j.rse.2021.112464

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1 Title:

- 2 Determining maximum entropy in 3D remote sensing height distributions and using it to
- 3 improve aboveground biomass modelling via stratification.

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17

18 Keywords

19 forest structure, forest aboveground biomass, Gini Coefficient, L-moments, airborne laser

- 20 scanning
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26 Abstract

McArthur's foliage height diversity (FHD) has been the gold standard in the determination of 27 structural complexity of forests characterized by LiDAR vertical height profiles. It is based on 28 Shannon's entropy index, which was originally designed to describe evenness in abundances 29 among qualitative typologies, and thus the calculation of FHD involves subjective layering 30 steps which are essentially unnatural to describe a continuous variable (X) such as height. In 31 this contribution we aim to provide a mathematical framework for determining maximum 32 entropy in 3D remote sensing datasets based on the Gini Coefficient of theoretical continuous 33 34 distributions, intended to replace FHD as entropy measure in vertical profiles of LiDAR heights (1D; X), with extensions to variables expressing dimensions of higher order (2D or 3D, $Z \propto$ 35 X^2 or X^3). Then we apply this framework to Boreal forests in Finland to describe landscape 36 heterogeneity with the intention to improve the modelling of forest aboveground biomass 37 (AGB), hypothesizing that LiDAR models of AGB should essentially be different in areas of 38 differing structural characteristics. We carried out a pre-stratification of LiDAR data collected 39 in 2012 using simple rules applied to the L-skewness (L_{skew}) and L-coefficient of variation of 40 LiDAR echo heights (L_{cv} ; equivalent to the Gini coefficient, GC_H), determining a new 41 threshold at $GC_H = 0.33$ as a consequence of the newly developed mathematical proofs. We 42 observed only moderate improvements in terms of model accuracies: RMSDs reduced from 43 41.7% to 38.9 or 37.0%. More remarkably, we identified critical differences in the metrics 44 selected at each stratum, which is useful to understand what predictor variables are more 45 important for estimating AGB at each area of a forest. We observed that higher LiDAR height 46 percentiles are more relevant at open canopies and heterogeneous forests, whereas closed 47 canopies in homogeneous forests obtain most accurate predictions from a combination of cover 48 metrics and percentiles around the median. Without stratification, the overall model would 49 neglect explained variability in the structural types of lower occurrence, and predictions from 50

a model influenced by structural types of higher occurrence would be biased at those areas.
These results are thus useful in terms of improving our understanding on the relationships
underlying LiDAR-*AGB* models.

54

55 **1. Introduction**

56 Structural complexity is an essential morphological trait of ecosystems, complementary to 57 others like vegetation height or cover (Schneider et al. 2017; Fahey et al. 2019; Valbuena et al. 2020), which is relevant to various ecological processes such as nutrients cycling, carbon 58 59 sequestration and species interactions (Brokaw and Lent 1999; Lindenmayer et al. 2000; McElhinny et al. 2005). There is however a lack of consensus on the most appropriate means 60 to measure the structural complexity of ecosystems (Neumann and Starlinger 2001; Lexerød 61 and Eid 2006), with approaches focused on measuring either entropy, e.g. Simpson or Shannon 62 indices (McArthur and McArthur 1961), or variability, e.g. variance or Gini coefficient (GC) 63 (Weiner 1990). The most popular approach follows the early works of McArthur and McArthur 64 (1961) who calculated the Shannon-based foliage height diversity (FHD) after layering the 65 ecosystem vertical profile into three strata, but there have been pleas for alternative measures 66 (Lovejoy 1972; Pearson 1975; Erdelen 1984; Weiner and Thomas, 1986; Valbuena et al. 2012). 67 This dichotomy has been reflected in the derivation of structural complexity measures from 68 LiDAR, with alternatives based on either layering the vertical profile (Lefsky et al. 2002a; 69 Vierling et al. 2008; Simonson et al. 2014; Weisberg et al. 2014; Listopad et al. 2015; Wilkes 70 et al. 2016; Almeida et al. 2019a; Bakx et al. 2019) or measuring variability in LiDAR heights 71 72 (Valbuena et al. 2017a; Moran et al. 2018; Mononen et al. 2019; Crespo-Peremarch et al. 2020; Hagar et al. 2020). 73

In this contribution we propose a mathematical framework (Appendix A) which effectively
merges both approaches, by showing how maximum entropy can be flagged up from values of

a variability measure such as the Gini coefficient. They constitute formal deductive proofs of 76 ideas that have previously been presented on the basis of empirical indications: such as a 77 78 threshold at GC = 0.5 employed to discriminate ecosystem structural heterogeneity (Valbuena et al. 2012, 2017a). Based on these mathematical developments, we further argue that different 79 thresholds apply for GC depending on whether calculated from LiDAR heights (GC_H) , or tree 80 basal areas (GC_{BA}) , because the former is a variable representing one dimension (X) and the 81 latter is an area, and thus bi-dimensional (X^2) (Appendix A). This mathematical framework 82 thus provides unified means for determining maximum entropy in the 3D space of information 83 provided by remote sensing tools such as LiDAR. 84

To quantify the amount of carbon sequestered by forests over large geographical areas, and use 85 86 them to inform global policies, it is important to attain reliable estimations of forest aboveground biomass (AGB) from local to global scales (Gibbs et al. 2007). In this context, 87 remote sensing in general, and LiDAR in particular, are the key technologies to monitor 88 reductions in emissions of greenhouse gases from deforestation and forest degradation (REDD) 89 (Boudreau et al. 2008; Asner et al. 2010). Airborne LiDAR produces detailed canopy 90 information (Maltamo et al. 2005; Gobakken and Næsset 2008) that provides opportunities for 91 predicting accurately various ecosystem attributes such as vegetation height (Magnussen et al. 92 93 1999; Maltamo et al. 2004; Koukoulas and Blackburn, 2005), tree diameters (Næsset, 2002; Räty et al. 2018), structural heterogeneity (Vierling et al. 2008; Weisberg et al. 2014; Adnan 94 et al. 2019), tree species (Van Aardt et al. 2008), or forest biomass and carbon (Næsset and 95 Gobakken 2008; Kronseder et al. 2012; Valbuena et al. 2017b). Metrics derived from airborne 96 LiDAR are the most promising information for efficient and accurate AGB prediction (Asner 97 and Mascaro 2014; Bouvier et al. 2015; Longo et al. 2017). For this reason, these metrics are 98 employed as auxiliary variables in airborne LiDAR-assisted estimations (Gobakken and 99 Næsset 2008; Asner et al. 2010). Mehtätalo and Nyblom (2009, 2012) developed the 100

relationship between canopy height obtained from airborne LiDAR data and forest attributes such as stand density and mean tree height, improving model-based estimations. However, we still lack information on the relationship between LiDAR metrics with the forest *AGB*, and how the predictive models are affected by forest structures (Drake et al. 2003; Knapp et al. 2020).

Researchers have developed a wide variety of LiDAR models estimating AGB stocked in 105 106 forests (Zolkos et al. 2013). The prediction error of the total AGB is dependent on the relationship between foliage observed by LiDAR and various AGB components (Lefsky et al. 107 2002b; Næsset and Gobakken 2008; Hernando et al. 2019). Thus, high heterogeneity in the 108 structural complexity of forests may cause difficulties in modelling (Drake et al. 2003; Hall et 109 al. 2005; Jaskierniak et al. 2011; Vincent et al. 2014). While there have been many attempts to 110 111 generalize LiDAR modelling of AGB (Asner and Mascaro 2014; Bouvier et al. 2015), a general relationship may not be appropriate for all regions, both even and uneven sized forests or dense 112 and sparse spatial structures (Vincent et al. 2014; Häbel et al. 2019; Knapp et al. 2020). To 113 overcome this difficulty, the forest area can be stratified into different development classes 114 (Næsset 2002) or forest structural types (FSTs) (Mascaro et al. 2011; Vincent et al. 2014), and 115 a separate model can be applied to each of them to obtain more reliable AGB estimations. With 116 these regards, we hypothesised that the Gini coefficient can be useful for such FST stratification 117 118 prior to modelling the forest AGB. Bollandsås and Næsset (2007) obtained reliable results following such approach with the support of field information (i.e., GC_{BA}). Alternatively, we 119 postulated that these FSTs could be detected directly from airborne LiDAR data (i.e. GC_H), and 120 apply a separate AGB model in each FST to improve AGB predictions. Based on results in 121 Valbuena et al. (2017a), we considered the use of L-moment ratios for such stratifications: L-122 coefficient of variation of LiDAR echo heights (L_{cv} ; equivalent to the Gini coefficient, GC_H) 123 and L-skewness (L_{skew}). We considered a new threshold at $GC_H = 0.33$ for separating even 124 sized from uneven sized forest structures, based on findings in Appendix A. Furthermore, 125

Valbuena et al. (2017a) also identified FSTs according to their light environment characteristics using the $L_{skew} = 0$ threshold which segregate the euphotic/open canopy and oligophotic/closed canopy forest areas (Lefsky et al. 2002a), by separating them as positive and negative skewness in between the [-1,1] bounds of L_{skew} . We evaluated the potential of these detected FSTs in improving the *AGB* prediction from the airborne LiDAR data.

131 In this article, we set the mathematical foundations for determining maximum entropy from a distribution of heights in 3D remote sensing (Appendix A), as an alternatively to common 132 binning procedures employed to determine McArthur and McArthur's (1961) FHD. Then we 133 employed this rationale, stratified the LiDAR-surveyed area according to the $L_{c\nu} = 0.33$ and 134 $L_{skew} = 0$ rules following Valbuena et al. (2017a), and carried out stratified sampling with 135 136 roughly equal sample sizes within each FST. The aim of this stratification was to evaluate the potential of FSTs to improve forest AGB predictions in the pre-stratified airborne LiDAR data 137 138 compared to the AGB predictions in the whole dataset without pre-stratification. We developed a general LiDAR-AGB model for the whole dataset without pre-stratification, and separate 139 FST-specific models at each stratum. We hypothesized that LiDAR models predicting AGB 140 should essentially be different in areas of differing structural characteristics. For this reason, 141 we also paid careful attention to the LiDAR metrics selected at each model, and used those 142 results to make inferences on the relationship behind the choice of metrics at each forest area, 143 with the intention to shed light on the effects of forest heterogeneity on LiDAR models 144 145 predicting AGB.

146 **2. Material and Methods**

149

147 2.1. Study Area and data collection

148This study was conducted in a 252,000 ha boreal forest located in the North Karelia region of

Finland (Figure 1). The dominant species in the study area are Norway spruce (*Picea abies* (L.)

Karst.), Scots pine (Pinus sylvestris L.) and Birch species (Betula spp.), and some other 150 deciduous species such as Alnus spp. and Populus spp. are also present. In May 2012, a Leica 151 ALS60 laser scanning system was used to collect airborne LiDAR data. Flight elevation was 152 2,300 m above ground level, which resulted in a scan density of 0.91 pulses per square meter. 153 The digital terrain model with 2 m resolution derived from the same LiDAR dataset was 154 provided by National Land Survey (Finland). The DTM was subtracted from the LiDAR echo 155 156 heights and area-based LiDAR metrics were computed using the FUSION software (Version 3.70, USDA Forest Service; McGaughey 2019). With the intention to get in the full structural 157 158 characteristics of forests and commensurate with forest data acquisition, a very small height threshold (< 0.1 m) was used to exclude ground echoes in the computation of area-based 159 metrics (Görgens et al. 2017). This eliminates ground echoes but consider seedlings and 160 saplings, which were included in the field inventory (Valbuena et al. 2016). Among the set of 161 FUSION metrics, two L-moment ratios were used for simulating a pre-stratification: L-162 coefficient of variation (L_{cv}) and L-skewness (L_{skew}) . The remaining metrics were involved in 163 the modelling of AGB. 164

165 ****approximate position of Figure 1*****

Field data for the calibration/validation of AGB models were jointly collected by the Finnish 166 Forest Centre (Suomen Metsäkeskus; SMK) and University of Eastern Finland (UEF) in 2013 167 (Valbuena et al. 2017a). There were 244 field plots in total from eight different strata and 168 sample size was approximately equal in each stratum. The stratification was based on the forest 169 development classes - seedling, sapling, young, advanced, mature, shelterwood, seed-tree and 170 multi-storey (Valbuena et al. 2016) -, determined on the basis of the SMK stand-wise 171 information from the previous forest management plan, randomly selecting plot locations over 172 areas covering each development class. Field data acquisition consisted in a concentric circle 173

design, recording species and diameter at breast height (dbh; cm) of trees within each 174 concentric plot according to its size (Valbuena et al. 2016). Tree heights (h; m) were measured 175 only for the basal area median tree of each species. For the even sized development classes 176 (young, advanced and mature), the field data were collected by SMK using a plot size of 9 m 177 radius for trees with dbh > 8 cm, while saplings were recorded within 5.64 m radius and 178 seedlings were counted using a 2.82 m long stick in distributed sub-plots (Figure 2). Plots 179 within the seed tree, shelterwood and multi-storey development classes were collected by UEF 180 using the same plot design. However, the size of the outer plot in these three development 181 classes was slightly increased to 9.77 m so that its size would become integer multiplier of the 182 inner subplots, which is convenient for the calculation of GC_{BA} following Valbuena et al. 183 (2013). For visual comparison of these development classes, mean leaf area density (LAD) 184 vertical profiles with 95% confidence intervals from all plots within each development class 185 186 were calculated from LiDAR data using the R package *LeafR* (Almeida et al. 2019b).

187 ****approximate position of Figure 2*****

188 2.2 Rule-based stratification of forest structural types using airborne lidar data

Postulating that LIDAR models of AGB should be essentially different in areas of differing 189 structural characteristics, we employed this dataset to simulate a pre-stratification scenario by 190 191 classifying the prediction area into FSTs detected directly from the LiDAR data. The study area was stratified using the abovementioned two L-moment ratios of airborne LiDAR height 192 distributions, and the rules were deduced from their mathematical properties instead of 193 inductive statistical distributions or supervised classification, thus absence of any field 194 information is involved (Valbuena et al. 2016). As L_{cv} is mathematically equivalent to the Gini 195 coefficient of LiDAR echo heights (GC_H) (Valbuena et al. 2017a), it could be used to describe 196 the structural properties related to the inequality in tree sizes within a forest area. $L_{cv} =$ 197

198 0.33 was used as a boundary line to discriminate forests with even-sized FSTs ($L_{cv} < 0.33$) 199 from uneven-sized ones ($L_{cv} > 0.33$), on the grounds that maximum entropy in the distribution 200 of LiDAR heights is reached at $L_{cv} = 0.33$ (**Appendix A**). Similarly, asymmetry (L_{skew}) 201 describes the structural heterogeneity related to light availability and tree size dominance 202 (Valbuena et al. 2017a). $L_{skew} = 0$, which represents the symmetric distribution of LiDAR 203 echo heights, was used to separate forests having oligophotic areas/closed canopy ($L_{skew} < 0$) 204 from euphotic areas/open canopy areas ($L_{skew} > 0$) (Lefsky et al. 2002a).

205 2.3 Aboveground biomass calculation from field data

R statistical software (R Core Team 2019) was used for all statistical analyses and modelling. Locally developed species-specific biomass equations were used to calculate tree aboveground biomass (agb; kg) for Scots pine and Norway spruce (Repola, 2009), and another for birch (Repola, 2008) which was used for all deciduous species. These were based on dbh and h, and thus individual tree heights were subsequently predicted using the Näslund's height curve (1936):

212
$$h = 1.3 + \left(\frac{dhb}{\beta_0 + \beta_1 dbh}\right)^{\alpha}, \qquad (1)$$

where the exponent was $\alpha = 2$ for pine and deciduous species, and $\alpha = 3$ for spruce. We 213 followed the methods suggested by Siipilehto (1999) in the estimation the Näslund's height 214 curve model parameters (β_0 , β_1) for each species. which included plot-level calibration with 215 species-specific diameter $(D_{\widetilde{ba}})$ and height $(H_{\widetilde{ba}})$ of the tree with median basal area (\widetilde{ba}) . Then 216 the species-specific parameters were used in the height curve model to predict the missing tree 217 heights from their dbh. Once calculated all the tree level agb values, they were aggregated to 218 plot level (AGB; Mg·ha⁻¹) according to their corresponding hectare expansion factors, and used 219 as a response variable in subsequent LiDAR models. 220

221 2.4 Modelling of aboveground biomass from airborne LiDAR data

Many airborne LiDAR derived metrics (predictors) were available for modelling the AGB. We 222 used function "regsubset" of the R package "leaps" (Lumley and Miller, 2017), which 223 performed a selection of the best subset of predictors using an exhaustive search among typical 224 LiDAR-AGB models (Valbuena et al. 2017b). We made an independent selection, the best 225 subset of predictors for the general model including the whole dataset (i.e. without 226 stratification), and also for each FST-specific model (even versus uneven sized forest 227 structures, and euphotic/open canopy versus oligophotic/closed canopy areas). Thereafter, 228 229 modelling based on the k-nearest neighbour (k-NN) method was used to predict the response variable (AGB) from the best subset of airborne LiDAR predictors (Mcinerney et al. 2010). We 230 used Euclidean distance with k = 5 in the k-NN implementation available in the R package 231 "YaImpute" (1.0-31 version; Crookston and Finley, 2008). 232

233 2.5 Accuracy assessment of aboveground biomass prediction

We used a 10-fold cross validation method for assessing the accuracy of the resulting models. The results of the general model and FST-specific models were evaluated and compared by means of their mean difference (*MD*) and root mean square difference (*RMSD*):

237
$$RMSD = \sqrt{\frac{\sum_{i=1}^{n} ((y_i^{cv} - \hat{y}_i)^2)}{n}},$$
 (2)

238
$$MD = \frac{\sum_{i=1}^{n} ((y_i^{cv} - \hat{y}_i))}{n},$$
 (3)

where *n* is the total number of observations (field plots), y_i^{cv} and \hat{y}_i are the predicted and observed value of *AGB* for observation *i*, respectively. Relative values (%) of *MD* and *RMSD* were obtained as the percentage over the mean observed *AGB*. As an additional quality control measure, we used a hypothesis test on the 1:1 correspondence between the observed (*obs_i*) and predicted (pre_i^{cv}) values from the intercept (α) and slope (β) of their linear regression (Leite and Oliveira, 2002; Piñeiro et al. 2008),

245
$$obs_i = \alpha + \beta pre_i^{cv},$$
 (4)

To avoid overfitting the models to the sample, the best subset procedure was constrained by additional restrictions to the sum of squares ratio (*SSR*), which evaluates the inflation in the unexplained variance when the model is not cross-validated (Valbuena et al. 2017b). *SSR* is the ratio between the squared root sum of the squares obtained by cross validation (SS^{cv}) and without cross validation (SS^{fit}).

251
$$SSR = \sqrt{SS^{cv}} / \sqrt{SS^{fit}},$$
 (5)

252
$$SS^{cv} = \sum_{i=1}^{n} (y_i^{cv} - \hat{y}_i)^2$$
(6)

253
$$SS^{fit} = \sum_{i=1}^{n} (y_i^{fit} - \hat{y}_i)^2$$
(7)

254 Where, \hat{y}_i is the observed value of the *AGB* for observation *i*, and y_i^{cv} and y_i^{fit} are the 255 predicted values using cross validation and without cross validation, respectively.

256 **3. Results**

257 *3.1. Airborne LiDAR based forest structural types*

Table 1 gives a development class-wise summary of plot-level characteristics calculated from the field data – density (*N*), quadratic mean diameter (*QMD*), above ground biomass density (*AGB*) and Gini coefficient of basal area (GC_{BA}) –, and also from the LiDAR data – Lcoefficient of variation (L_{cv} ; equivalent to the Gini coefficient, GC_H) and L-skewness (L_{skew}). of LiDAR return heights –. Height profiles of each development class calculated from LiDAR data are given in **Figure 3**, which shows mean changes in LAD through the vertical profiles at each development class. **Figure 4** further shows how different forest structural types detected

directly from airborne LiDAR data are distributed either sides of the $L_{cv}(GC_H) = 0.33$ and 265 $L_{skew} = 0$ thresholds. Some structural dynamics can be observed from these figures, since the 266 majority of areas in seedling development classes were separated as even sized by $L_{cv}(GC_H) <$ 267 0.33, because they are very small and roughly equal in size at first, to later more inequality in 268 diameter distribution toward the sapling stage ($L_{cv}(GC_H) > 0.33$) (Figure 4a). Likewise, the 269 young, advanced and mature development classes which mostly contain equality in 270 diameter/basal area distribution were mostly separated as even sized ($L_{cv}(GC_H) < 0.33$). Seed 271 trees and multi-storied development classes have higher inequality in their diameter 272 273 distribution, they show high dispersion in their LiDAR echoes, and thus they were separated as uneven sized structure ($L_{cv}(GC_H) > 0.33$). Similarly, in Figure 4b most seedling and 274 sapling development classes were separated as euphotic areas $(L_{skew} > 0)$ because their 275 276 canopies have not closed yet at these stages of development. As they grow and increase in AGB through young, advanced and mature development classes, they shift toward oligophotic areas 277 with closed canopies and negative skewness of LiDAR return heights ($L_{skew} < 0$). The 278 shelterwood development class which has a dense overstory and high LiDAR returns was 279 classified as oligophotic ($L_{skew} < 0$), whereas seed-tree areas and multi-storey development 280 classes with sparse overstorey were mainly classified as euphotic ($L_{skew} > 0$). 281

- 282 ***approximate position of Table 1****
- 283 ***approximate position of Figure 3****
- 284 ****approximate position of Figure 4*****

We were then interested on whether the different thresholds that **Appendix A** shows for LiDAR heights ($GC_H(L_{cv}) = 0.33$) and field data ($GC_{BA} = 0.5$) would segregate forests with similar structural properties. **Figure 5** shows a comparison of aggregated diameter distributions (plus basal area-weighted distributions, in darker colors in the background) with confidence

intervals. The difference between the distribution of proportions in density of stems versus 289 basal area highlights structural differences which cannot be easily appreciated in diameter 290 291 distributions, since in highly complex structures with large differences in tree sizes the proportion of basal area taken by larger trees becomes predominant. This could be appreciated 292 in the distributions of strata yielded from the LiDAR data only $(GC_H(L_{cv}) < 0.33)$ and 293 $GC_H(L_{cv}) > 0.33$, respectively in Figures 5a and b), as much as it was for the distributions 294 yielded when the strata was generated using the field data itself ($GC_{BA} < 0.50$ and $GC_{BA} >$ 295 0.50, respectively in Figures 5c and d). These results emphasize the reliability of a purely 296 LiDAR-based classification in the structural heterogeneity assessment of forests. 297

298 ***approximate position of Figure 5****

299 3.3. Best-subset variable selection

In order to facilitate direct comparison of all models, we fixed the number of LiDAR predictors 300 to be six for all models, based on the SSR restriction of the best-subset procedure which assured 301 that none of them had over-fitting effects, plus a positive outcome in the hypothesis test of 1:1 302 correspondence. Table 2 shows the variables selected at each of them: the general model 303 developed for the whole data without pre-stratification, and each FST-specific model 304 developed for the even and uneven sized forest structures and oligophotic/closed canopy and 305 euphotic/open canopy areas, obtained from the direct classification of airborne LiDAR data. 306 While all the selected predictors were those typically included in LiDAR-AGB modelling -307 308 averages (e.g. quadratic or cubic means), dispersion statistics (e.g., variance), percentiles, and cover metrics (i.e. percentages above thresholds) of LiDAR return heights -, we identified 309 critical differences in the metrics selected at each stratum, which is useful to understand what 310 predictor variables are more important for estimating AGB at each area of a forest. We observed 311 that higher LiDAR height percentiles were more relevant at open canopies and heterogeneous 312

forests, whereas closed canopies in homogeneous forests obtained a best subset based on 313 combinations of cover metrics and percentiles around the median. In the uneven-sized 314 structures, higher percentiles, variance and absolute average deviation of LiDAR return heights 315 were selected. On the other hand, in the even-sized stratum the model included the mode, 316 L_{skew} , the median, and cover metrics (percentage of all returns above mode and total first 317 returns). Similarly, in the oligophotic/closed canopy areas, the median and cover metrics were 318 important, while in the euphotic areas/open canopy areas, higher percentiles and mean absolute 319 deviation from median and variance were selected. Thus, the similarities of even-sized with 320 321 oligophotic areas on one hand, and uneven with euphotic areas observed in Figure 4, showed an influence in the modelling itself (Table 2), thus indicating convergence in the relationships 322 between structure and modelling results. 323

324 ****approximate position of Table 2*****

325 *3.3. Modelling aboveground biomass from airborne LiDAR based forest structural types*

326 The AGB was predicted in each model using the associated best subset of LiDAR predictors, 327 and their accuracies were assessed. In the general model (Table 3 and Figure 6), i.e. a model 328 fitted using the whole dataset, the RMSD between the observed and predicted AGB was 37.4 Mg·ha⁻¹. We disaggregated these accuracy statistics by strata, to allow direct comparison with 329 the FST-specific models, which resulted in 37.1 and 37.6 Mg·ha⁻¹ respectively in the even and 330 uneven-sized forest areas and resulted in 37.6 and 37.3 Mg·ha⁻¹ in oligophotic and euphotic 331 areas, respectively. In relative terms, the general model RMSD 41.7%, which seems high 332 because of the inclusions of seedling and sapling areas of very low AGB in the dataset. The 333 general model showed some bias when applied to specific FSTs, as it can be appreciated by 334 underpredictions of around 4.8-5.5% in terms of their MDs, with the even-sized forests being 335 the only areas where not such strong bias effect was observed (-2.33% only). 336

337 ****approximate position of Table 3*****

338 ****approximate position of Figure 6*****

The results for the FTS-specific models are summarized in Tables 4a-b, and the scatterplots in 339 Figures 7-8. The RMSD improved both in the even sized (34.6 Mg·ha⁻¹) and uneven sized 340 (35.3 Mg·ha⁻¹) forest structures (**Table 4a**) as compared to the general model (**Table 3**). The 341 MD similarly improved in the uneven sized forest structure (-2.72 Mg·ha⁻¹) and only slightly 342 decreased in the even sized areas (-2.30 Mg·ha⁻¹). These specific models developed for the even 343 and uneven sized forest structures also showed an improvement in the MD and RMSD when 344 aggregated for the whole area (-2.52 and 34.9 Mg·ha⁻¹) (**Table 4a**), compared to the general 345 model (-3.55 and 37.4 Mg·ha⁻¹) (**Table 3**). Similar improvements in the MD and RMSD were 346 observed in the FST specific models developed for the oligophotic/closed canopy areas (-2.22, 347 33.5 Mg·ha⁻¹), euphotic areas/open canopies (-2.52, 32.9 Mg·ha⁻¹), and whole data (-2.37, 33.2 348 Mg·ha⁻¹) (**Table 4b**). All the FST-specific modelling approaches, thus, showed improvements 349 350 compared to the general model both in terms of unbiasedness and improving the precision of 351 predictions.

- 352 ****approximate position of Table 4*****
- 353 ****approximate position of Figure 7*****
- 354 ****approximate position of Figure 8*****
- 355 4. Discussion

4.1. Determining maximum entropy from a distribution of heights in 3D remote sensing

In previous contributions we have showed a threshold of interest which flags up maximum entropy at the Gini Coefficient value of $GC_{BA} = 0.50$ (Valbuena et al. 2012, 2017). This

threshold allows to compare the entropy of the ecosystem using a statistic of dispersion, arguing 359 that is more correct for continuous variables because it avoids the factitious binning step 360 required when computing foliage height diversity (McArthur and McArthur, 1961), based on 361 Shannon's entropy index which was originally meant for discrete variables (Shannon, 1948). 362 It is important to note that this threshold is applicable for a Gini coefficient of a Lorenz curve 363 representing differences in basal area among trees growing within a given area (GC_{BA}) 364 (Valbuena et al. 2012). On the other hand, in this contribution we further argue that for a Gini 365 coefficient of a Lorenz curve representing differences in LiDAR heights within that same area 366 (GC_H) , the alternative value of $GC_H = 0.33$ should be the one used instead to identify maximum 367 entropy. The reason is that height is a one-dimensional variable (X), whereas basal areas are 368 two-dimensional (X^2) . In order to achieve these generalized conclusions, we need to use 369 theoretical distribution functions and show how their parameters propagate into Lorenz curves 370 and values of the Gini Coefficient directly dependent on those parameters. In the Appendix A, 371 we show formal proofs for these values obtained from theoretical distributions, to illustrate the 372 reasoning employed in this contribution. We also show how these maxim entropy values of 373 GC_X extend to higher dimensions (e.g. GC_{X^2}), thus developing a mathematical framework 374 which provides unified means for determining maximum entropy in the 3D space of 375 information provided by remote sensing tools such as LiDAR. Figure 5 illustrates empirically 376 the equivalence of the LiDAR and field approaches. 377

378 *4.2. Rule-based pre-stratification into different forest structural types*

Airborne LiDAR explains the key characteristics of forests related to the structural heterogeneity that can be relevant to describe tree size hierarchy (Valbuena et al. 2013), vegetation growth (Stark et al. 2012) and light availability (Lefsky et al. 2002a). Advancement in airborne LiDAR remote sensing promises reliable accuracies in the prediction of biophysical

stand properties (Lefsky et al. 2002b; Valbuena et al. 2020) and various studies have evaluated 383 and found that the pre-stratification of forests using airborne LiDAR can improve the attribute 384 385 estimation (Næsset 2002; Maltamo et al. 2015) and reduce the sampling efforts (Papa et al. 2020). Following the same concept but using solely the LIDAR data as opposed to using field 386 information, in this study different FST were obtained from the direct classification of airborne 387 LiDAR data. We applied rule-based pre-stratifications and used $L_{cv}(GC_H)$ and L_{skew} of the 388 LiDAR echo heights which are the two prominent LiDAR metrics in separating the even from 389 uneven sized structures and oligophotic/closed canopy from euphotic/open canopy forest areas, 390 respectively (Valbuena et al. 2017a). In Figure 4a, we found that the young, advanced and 391 mature development classes which have similar diameters and basal areas distributions 392 393 $(GC_{BA} < 0.5)$ usually backscatter most of the LiDAR returns and hold smaller variance in their height values were mostly separated by the lower values of $L_{cv}(GC_H) < 0.33$. There is a 394 consistency on results in Table 1 showing that LiDAR values of GC_H are reflected by higher 395 values in GC_{BA} , with the proofs in Appendix A being the explanation for this effect. A notable 396 exception is observed in the case of the sapling development, which showed a high uncertainty 397 in terms of GC, with a wide range of values in both GC_{BA} and GC_H (Table 1). This is the reason 398 that L_{skew} was important to add as an additional LiDAR metric because the similarity between 399 GC_{BA} (Valbuena et al. 2013) and GC_H (L_{cv}) only occurs if the higher values of GC is due to the 400 presence of canopy gaps which allow large a portion of laser pulses to pass and disperse in the 401 canopy (Stark et al. 2012, Valbuena et al. 2017a). Thus, by looking at the L_{skew} values, the 402 sapling was separated as euphotic/open canopy areas ($L_{skew} > 0$) which could be the reason 403 of the higher L_{cv} values. Other development classes such as seed-tree and multi-storey areas 404 were separated as even sized by both GC_{BA} (0.73 and 0.92) and GC_H ($L_{cv} = 0.58$ and 0.58), 405 however, the shelterwood development class wherein the mean GC_{BA} was 0.95 was not 406 properly separated and many plots were below $L_{cv}(GC_H) = 0.33$ (Figure 4 and Table 1). This 407

might be due to the omission of the understory vegetation by the lower point density of the ALS data in our study area (0.91 points.m⁻²) and any pointy density lower than at least 3 points.m⁻² are unsuitable for the structural heterogeneity assessment, using the *GC* in particular (Adnan et al. 2017). Thus, the disintegration of such classes could further be improved by increasing the pulse density of the LiDAR data (Gobakken and Næsset 2008; Ruiz et al. 2014).

When laser pulses hit a closed canopy vegetation, only a small portion of pulses penetrate the 413 canopy, which is represented by LiDAR height distributions with negative asymmetry L_{skew} < 414 0. This also indicates the shady/oligophotic areas where only a smaller portion of light will 415 416 reach the ground, for example, young, advance and mature development classes. Similarly, areas where smaller portion of LiDAR returns due to the presence of sparse vegetation denotes 417 the open/euphotic areas which were detected by $L_{skew} > 0$, for example, seedlings, saplings, 418 seed trees, shelterwood and multi-storey (Figure 4b and Table 1). Figure 5 further highlights 419 the importance of this rule-based classification and presents an adequate comparison between 420 the even and uneven sized forest structures separated by the $GC_H(L_{cv}) = 0.33$, or $GC_{BA} = 0.5$ 421 (Appendix A). In this figure, it is clear that the diameter and basal area weighted distributions 422 in both even sized and uneven sized structure which are obtained from the GC_H (Figure 5a and 423 **5b**) and GC_{BA} (Figure 5c and 5d) are very similar and the small differences are due to missing 424 detection of seedling in the smallest size class. This provides further insights that GC_H is an 425 appropriate option to separate structural heterogeneity of forest. 426

427 4.3 Selection of best subsets of airborne LiDAR predictors in the AGB prediction models

Various alternatives are used to select the optimum number of parameters (predictors) to
predict a response variable such as best subset, stepwise, and nearest neighbor (MSN) selection
methods (Næsset et al. 2002; Van Aardt et al. 2008; Asner et al. 2010; Valbuena et al. 2017b,
Almeida et al. 2019a). We used the best subset method which because the selection of a given

variable is independent of interactions among variables as they are selected (Hudak et al. 2006). 432 Thus, the selection of the six predictors was independent from the other LiDAR metrics and 433 the different modelling options, yet reaching several convergences. Minimizing the number of 434 meaningful predictors that describe various aspects of the forest structures is an important 435 consideration (Hudak et al. 2006, Asner and Mascaro 2014; Vincent et al. 2014; Bouvier et al., 436 2015; Valbuena et al. 2017b), and our selection of six predictors to allow model comparison 437 438 (Table 2) was a compromise balance between model error and overfitting that worked well for all the options. The results obtained in variable selection are as valuable as the accuracy 439 440 assessment itself, since it shows convergences between some areas of the forest and discrepancies between opposing FSTs. They also show which FSTs influence more the general 441 model, with effects both in the overall error but also biasing effects in the areas of the forest 442 that had a lower influence in the composition of the general model. Cover metrics were 443 important in all model but more predominant in oligophotic areas. The variance of LiDAR 444 return heights was only selected in the uneven sized structures and euphotic/open canopy areas. 445 Different height percentiles were influential in different FST-specific models, with the median 446 (50th height percentile) being important in the even sized and oligophotic structures, and higher 447 percentiles (70th or 99th, representing dominant trees) becoming selected in the uneven sized 448 449 structure and euphotic areas (Adnan et al. 2017). Most importantly, the variables selected in the general model were highly influenced by the even-sized areas of the forest, with both 450 451 models presenting large similarities (Table 2), which is a good explanation for the results observed in the accuracy assessment, since the general model showed lesser error in those areas 452 and high levels of biasness in the remaining FSTs. All these demonstrate the superiority of 453 obtaining FST-specific models to predict forest AGB from LiDAR, as opposed to approaches 454 seeking a single model valid for all forest areas. 455

456 *4.4 Comparison of the aboveground biomass predicted in the whole data without stratification*457 *and each pre-stratified FSTs*

In addition to the typical statistics employed to evaluate the quality of *AGB* predictions, namely 458 459 MD and RMSD (Van Aardt et al. 2008; Kankare et al. 2013; Straub et al. 2013; Räty et al. 2018), we also employed an evaluation of the inflation of error in cross-validation (the SSR) 460 and hypothesis test of 1:1 correspondence between observed and predicted AGB to enhance the 461 reliability of our resulting models (Valbuena et al. 2017b). Considering the results obtained for 462 whole dataset with either alternative, the 37.4 Mg \cdot ha⁻¹ *RMSD* of the general model (**Table 3**), 463 was improved by the FST-specific model approaches, reaching 34.9 Mg·ha⁻¹ (**Table 4a**), and 464 33.2 Mg·ha⁻¹ (Table 4b). Considering results obtained by FST, all figures also show 465 improvements, even and even-sized areas where RMSDs improved from the 37.1 Mg·ha⁻¹ 466 (Table 3) to 34.6 Mg·ha⁻¹ (Table 4a), with only a slight increase in *MD*. This is very important, 467 as otherwise result in FST-wise MDs for the general model showed bias effects in forest areas 468 highly structured. This is explained by the higher influence that even-sized areas had in the 469 470 general model, possibly because LiDAR metrics have a larger explanatory capacity for AGB in these areas, thus showing potential harmful consequences in AGB modelling approaches 471 neglecting the effects of forest structure. While the accuracies in AGB prediction improved 472 only moderately in the FST-specific models as compared to the general model, the differences 473 474 observed in the selection of airborne LiDAR predictors in each model can be critical, as they can produce biased results at specific areas of the forest. We thus encourage the prior 475 classification into different FSTs for selecting the most relevant LiDAR predictors at each area 476 477 of the forest, which besides of improving the estimation of AGB could provide important ecological insights on forest dynamics such as regeneration (Valbuena et al. 2013), self-478 thinning (Coomes and Allen, 2007) or productivity (Bourdier et al. 2016), and reduce the 479 480 sampling efforts needed for a given level of accuracy (Papa et al. 2020), assisting in better 481 forest inventory, management and planning (Næsset 2002; Maltamo et al. 2015). Thus, the 482 improved *AGB* prediction approach is suitable for purposes such as quantification of carbon 483 stock for REDD activities for a large forest area, but also for a better forest management, 484 planning and understanding of the natural dynamics within a large forest area.

485 **5.** Conclusions

Our results demonstrate the superiority of obtaining FST-specific models to predict forest AGB 486 from LiDAR, as opposed to approaches seeking a single model valid for all forest areas. We 487 recommend the use of LiDAR information to pre-stratify the forest area prior to the field 488 489 campaign, so that forest data acquisition can be tailored to the structural characteristics of the area. In order to determine these structural characteristics, we defended the use of GC above 490 the use of FHD, being less computationally demanding but also conceptually better. Appendix 491 A provides a mathematical framework for determining maximum entropy in 3D remote sensing 492 datasets based on the GC of theoretical continuous distributions, intended to replace FHD as 493 494 entropy measure in one-dimensional LiDAR vertical profiles (1D), with extensions to higher 495 order dimensions bi- or three-dimensional (2D or 3D).

496 Acknowledgements

497 Syed Adnan's PhD is funded by National University of Sciences and Technology (NUST), 498 Pakistan under FDP 2014-15. Noemi L. Ammaturo worked at the Department of Plant Sciences 499 supervised by Rubén Valbuena, under The Cambridge Earth System Sciences Doctoral 500 Training Partnerships (Cambridge ESS DTP, reference NE/L002507/1), which is a scheme 501 funded by the UK Natural Environment Research Council (NERC). We would like to thank the 502 Editor-in-Chief, Associate Editor and three reviewers for their comments and suggestions for 503 the manuscript.

Appendix A. Proofs for maximum entropy thresholds corresponding to $GC_X = 0.33$ and $GC_{X^2} = 0.50$.

507 Let X be a random variable taking values in the set of positive numbers, and E[X] its expectation. Let $f_X(x)$ and $F_X(x)$ be their probability density function (p.d.f.) and cumulative 508 distribution function (c.d.f.), respectively, and further let $F_X^{-1}(p)$ be the quantile function 509 (inverse of the c.d.f.; its generalized definition is $F_X^{-1}(p) = inf\{x: p \le F(x)\}$). The Lorenz 510 curve $L_X(p)$ specifies the accumulated proportion of the total of X that is attributed to a given 511 512 accumulated share of the population ordered by increasing X. Thus, the Lorenz curve provides a mapping from interval [0,1] to interval [0,1], where the domain includes the proportion from 513 the ordered population and the codomain the share of X. The Lorenz curve can be written as 514

515 (A.1)
$$L_X(p) = \frac{\int_0^p F^{-1}(t)dt}{E[X]}$$
, for $0 \le p \le 1$

516 The Gini coefficient is the twice area between the Lorenz curve and the diagonal line $L_X(p) =$ 517 *p*, which is thus assessed with the integral:

518 (A.2)
$$GC_X = 1 - 2 \int_0^1 L_X(p) dp$$

The Lorenz curve for aX for a positive constant a is the same as that of X. Therefore the Lorenz curve and Gini coefficient have the property of being invariant under linear scaling of X by a positive constant.

In applications using the distribution LiDAR heights X = H, the Lorenz curve $L_H(p)$ specifies the proportion of total accumulated heights at the 100*p* % of lower (or higher) vertical strata. In forest science, from the distribution of tree diameters X = D, the Lorenz curve $L_D(p)$ gives the proportion of total accumulated diameters for the 100*p* % smallest (or largest) trees. It is however more common to use variables which are logical to accumulate, such as basal area X = BA or above-ground biomass X = AGB, as it is more useful to know the proportion of basal area or biomass accumulated from for the 100*p* % smallest (or largest) trees. These variables are however never measured directly, and instead derived from a transformation of *D* or *H*, or both (Mehtätalo and Lappi, 2020). The following proofs demonstrate: (1) the threshold $GC_x = 0.33$ denotes maximum entropy for unidimensional measures, i.e. *D* or *H*; and (2) that this value of maximum entropy for *D* derives into $GC_{X^2} = 0.50$ for the transformed variable $Z = X^2$, namely the bi-dimensional measure *BA*, as it was empirically devised in Valbuena et al. (2012).

535

536 *Proofs for the Lorenz curve and Gini Coefficient of a uniformly distributed variable*

537 *(maximum entropy)*

The continuous uniform distribution $U(x_{\text{max}}, x_{\text{min}})$ has equal probability density for any u-538 length interval [x, x + u] within the range $X \in [x_{\min}, x_{\max}]$. It has the maximum entropy 539 540 among all continuous distributions which have the same range (Sung and Bera, 2009). Thus, for a given range $\theta = x_{max} - x_{min}$ and a given number of strata θ/u considered, the uniform 541 542 distribution yields the maximum value of Shannon's (1848) entropy index (Valbuena et al. 2012). In applications using LIDAR heights, this is a vertical profile showing even proportions 543 for all strata, yielding a maximum value for McArthur & McArthur's (1961) foliage height 544 diversity, with $x_{\min} = 0$ being the ground level and $x_{\max} = \theta$ being the maximum height of 545 vegetation. 546

547 The continuous uniform distribution $X \sim U(0, \theta)$ has the p.d.f.:

548 (A.3)
$$f_X(x;\theta) = \begin{cases} 1/\theta, \text{ for } 0 \le x \le \theta\\ 0, \text{ otherwise} \end{cases}$$

549 The c.d.f. is:

550 (A.4)
$$F_X(x;\theta) = \begin{cases} 0, \text{ for } x < 0 \\ x/_{\theta}, \text{ for } 0 \le x \le \theta \\ 1, \text{ for } \theta \le x \end{cases}$$

551 The quantile function and expected value are:

552 (A.5)
$$F_X^{-1}(p) = \theta p$$

553 (A.6)
$$E[X](=\mu) = \frac{\theta}{2}$$

554 Substituting these in Eq. (A.1), the Lorenz curve becomes (Figure A.1):

555 (A.7)
$$L_X(p) = \frac{\int_0^p \theta t \, dt}{\theta/2} = \frac{\theta p^2/2}{\theta/2} = p^2$$

556 And thus, substituting in Eq. (A.2), the Gini coefficient of a uniform distribution becomes:

557 (A.8)
$$GC_X = 1 - 2\int_0^1 p^2 dp = 1 - \frac{2}{3} = \frac{1}{3}$$

Hence, any variable X that has the minimum of zero and is distributed evenly along all its values, such as D or H, would have $GC_X = 0.33$, which thus is the value of Gini Coefficient which corresponds to maximum entropy.

562 Proofs for the Lorenz curve and Gini Coefficient of the second power of uniformly distributed
563 variable

Next, we will proceed to deduce the Lorenz curves $L_{BA}(p)$ and Gini coefficient GC_{BA} values for basal areas that derive from this situation of maximum entropy in the distribution of tree diameters. The basal area is directly calculated from a transformation of the diameters $BA = aD^2$. As per the scale-invariability property of Lorenz curves the scalar *a* can be further disregarded, and thus we now consider the Lorenz curve and Gini coefficient of transformation $Z = X^2$ when $X \sim U(0, \theta)$.

570 The c.d.f. and p.d.f of the transformed variable are:

571 (A.9)
$$F_{X^2}(z;\theta) = \begin{cases} 0, \text{ for } z \le 0\\ \sqrt{z}/_{\theta}, \text{ for } 0 \le z \le \theta^2\\ 1, \text{ for } z \ge \theta^2 \end{cases}$$

572 (A.10) $f_{X^2}(z;\theta) = \begin{cases} \frac{1}{2\theta\sqrt{z}}, & \text{for } 0 \le z \le \theta^2 \\ 0, & \text{otherwise} \end{cases}$

573 Thus, the quantile function and expected value of Z are:

574 (A.11)
$$F_{X^2}^{-1}(p) = \theta^2 p^2$$

575 (A.12)
$$E[X^2] = \frac{\theta^2}{3}$$

576 Substituting these in Eq. (A.1), the Lorenz curve becomes (Figure A.1):

577 (A.13)
$$L_{X^2}(p) = \frac{\int_0^p \theta^2 t^2 dt}{\theta^2/3} = \frac{\theta^2 p^3/3}{\theta^2/3} = p^3$$

578 And thus, substituting in Eq. (A.2), the Gini coefficient of a uniform distribution becomes:

579 (A.14)
$$GC = 1 - 2\int_0^1 p^3 dp = 1 - \frac{2}{4} = \frac{1}{2}$$

Hence, for any variable $Z \propto X^2$ that is proportional to the second power of X, such as of BA

is to *D*, the
$$GC_{X^2} = 0.50$$
 corresponds to the maximum entropy of *X*.

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Tables

Table 1. Aboveground biomass and other forest attributes calculated at each forest development class.

			AGB	QMD		Ν	GC _H	
			(Mg·ha ⁻¹)	(cm)	<i>GC_{BA}</i>	(trees·ha ⁻¹)	/ L _{cv}	Lskew
		Min	2.48	0.10	0.00	13909	0.07	0.14
	Soodlings	Mean	7.96	0.10	0.00	44770	0.23	0.31
	Securings	Max	28.51	0.10	0.00	182522	0.54	0.70
		SD	5.14	0.00	0.00	32987	0.09	0.13
		Min	6.14	0.10	0.00	1601	0.20	-0.18
	Saplings	Mean	34.88	3.05	0.35	31852	0.42	0.21
		Max	112.48	6.93	0.89	110774	0.60	0.59
		SD	24.62	1.78	0.29	24754	0.12	0.20
		Min	13.09	6.23	0.25	864	0.15	-0.36
	Voung	Mean	79.91	10.00	0.43	3254	0.29	-0.11
	Toung	Max	160.01	14.44	0.66	6523	0.58	0.33
		SD	31.67	2.18	0.09	1475	0.11	0.17
		Min	49.56	12.68	0.15	314	0.09	-0.41
Development Class	Advanced	Mean	96.98	17.27	0.42	1003	0.28	-0.20
	Auvanceu	Max	182.76	22.15	0.63	2082	0.50	0.14
		SD	30.26	2.63	0.14	462	0.10	0.13
	Mature	Min	73.75	16.07	0.19	314	0.09	-0.48
		Mean	179.07	23.35	0.49	844	0.23	-0.21
		Max	410.55	32.44	0.68	1807	0.41	0.00
		SD	76.81	4.60	0.17	374	0.08	0.11
	Shelterwood	Min	23.15	3.32	0.79	9020	0.21	-0.36
		Mean	171.01	5.63	0.95	33935	0.36	0.07
	Shellerwood	Max	305.34	9.25	1.00	108805	0.57	0.26
		SD	83.39	1.65	0.06	24028	0.10	0.15
	Seed Trees	Min	23.65	2.29	0.11	117	0.14	-0.23
		Mean	70.43	14.76	0.73	9833	0.58	0.37
		Max	143.52	38.14	0.99	39601	0.85	0.90
		SD	28.29	12.14	0.35	11209	0.21	0.31
		Min	17.99	1.41	0.68	2219	0.20	-0.22
	Multi-	Mean	77.02	3.87	0.92	33279	0.58	0.30
	Storied	Max	271.39	9.60	0.99	78131	0.84	0.83
		SD	54.73	2.19	0.09	16382	0.16	0.30

AGB: aboveground biomass; *QMD*: quadratic mean diameter; GC_{BA} : Gini coefficient of basal area; GC_H : Gini coefficient of LiDAR; L_{cv} : L-coefficient of variation of LiDAR heights; L_{skew} : L-skewness of LiDAR heights SD: standard deviation

Table 2. Airborne LiDAR predictors selection (best subset) for the general model (whole data without pre-stratification) and each forest structural type specific model (even sized, uneven

without pre-stratification) and each forest structural type specific model (even sized,sized, oligophotic/closed canopy and euphotic/open canopy forest structures).

Predictors	General $GC_H(L_{cv})$		(L_{cv})	L _{skew}	
	Model	Even	Uneven	Oligophotic	Euphotic
		(<0.33)	(>0.33)	(<0)	(>0)
Variance	*		*		*
Median of the absolute deviations	*	*		*	
(MAD) from the overall mode	•			·	
MAD from the overall median					*
L.skewness		*			
Average absolute deviation (AAD)			*		
Cubic mean					*
Quadratic mean		*			
25th height percentile	*				
50th height percentile	*	*		*	
60th height percentile					*
70th height percentile			*		
99th height percentile			*		*
% first returns above 0.1m			*		
% all returns above 0.1 m				*	
% all returns above mean				*	
% first returns above mode		*		*	
Ratio returns above 0.1 m /	*	*	*		*
total first returns	•	•	•		·
Canopy relief ratio	*			*	

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Table 3. Accuracy assessment of the observed and predicted aboveground biomass of thegeneral model.

	Whole -	$GC_{H}(L_{cv})$		L _{skew}	
	Data	Even (<0.33)	Uneven (>0.33)	Oligophotic (<0)	Euphotic (>0)
Sample size	244	120	124	119	125
MD	-3.55	-2.09	-4.97	-4.56	-4.31
MD (%)	-3.95	-2.33	-5.54	-5.08	-4.81
RMSD	37.4	37.1	37.6	37.6	37.3
RMSD (%)	41.7	41.4	41.9	41.9	41.6
SSR	1.03	1.02	1.04	1.04	0.98

872 $GC_H(L_{cv})$: Gini coefficient/L-coefficient of variation of LiDAR heights; L_{skew} : L-skewness of

LiDAR heights; MD: mean difference; RMSD: relative mean square difference;.

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Table 4. Accuracy assessment of the observed and predicted aboveground biomass of eachforest structural type specific models.

	Whole Data	$GC_{H}(L_{cv})$		
	whole Data	Even (<0.33)	Uneven (>0.33)	
Sample size	244	120	124	
MD	-2.52	-2.30	-2.72	
MD (%)	-2.81	-2.57	-3.03	
RMSD	34.9	34.6	35.3	
RMSD (%)	38.9	38.6	39.4	
SSR	0.97	0.96	0.99	

878 (a) Even versus uneven-sized structure

(b) Oligophotic/closed canopy versus euphotic/open canopy areas

		L _{ske}	?W
	Whole Data	Oligophotic (<0)	Euphotic (>0)
Sample size	244	119	125
MD	-2.37	-2.22	-2.52
MD (%)	-2.64	-2.48	-2.81
RMSD	33.2	33.5	32.9
RMSD (%)	37.0	37.4	36.7
SSR	0.98	0.98	0.98

 $\overline{GC_H(L_{cv})}$: Gini coefficient/L-coefficient of variation of LiDAR heights; L_{skew} : L-skewness of

LiDAR heights; MD: mean difference; RMSD: relative mean square difference; SSR: sum ofsquare ratio.

893 Figure Captions











924 Figure 3. Mean leaf area density (LAD) profiles calculated directly from LiDAR data for each development class (a) Sapling (b) Young (c)

925 Advanced (d) Mature (e) Shelterwood (f) Multi-storey and (g) Seed trees. Lines show mean LAD of all plots and grey areas their 95%

926 confidence intervals.







929 Figure 4. Distribution of different forest development classes on either side of the (a) 930 $L_{cv}(GC_H) = 0.33$ and (b) $L_{skew} = 0$.



Figure 5. Comparison of diameter and basal area distribution in the even and uneven sized forest structural types separated by Gini coefficient of LiDAR ($GC_H(L_{cv}) = 0.33$) (a, b) and Gini coefficient of basal area ($GC_{BA} = 0.5$) (c, d).



937	Figure 6. Observed vs predicted aboveground biomass (Mg·ha ⁻¹) plots of the kNN imputation
938	method using general model for (a) whole data without pre-stratification and each forest
939	structural types obtained directly from airborne LiDAR classification such as (b) even sized,
940	(c) uneven sized, (d) oligophotic/closed canopy and (e) euphotic/open canopy. The red line
941	represents 1:1 correspondence and the black line shows linear regression fit between observed
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Figure 7. Observed vs predicted aboveground biomass (Mg·ha⁻¹) plots of the kNN imputation method using specific models developed for (a) even sized and (b) uneven sized forest structure and their combination for the (c) whole data. The red line represents 1:1 correspondence and the black line shows linear regression fit between observed and predicted values.





Figure 8. Observed vs predicted aboveground biomass (Mg·ha⁻¹) plots of the kNN imputation method using specific models for (a) oligophotic areas/closed canopies and (b) euphotic areas/open canopies and their combination for the (c) whole data. The red line represents 1:1 correspondence and the black line shows linear regression fit between observed and predicted values.





966 Figure A1. Lorenz curves of maximum entropy for X, and its transformed variable $Z \propto X^2$.